

SYNTHESIS AND SEARCH FOR PARADIGMS IN WETLAND ECOLOGY

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This book contains observations on the forested wetlands in over 50 countries by 16 contributors. Chapters review an extensive literature and discuss many patterns of forested wetland response to environmental factors. The bulk of information on forested wetlands from many parts of the world tends to be floristic (e.g., Ch. 12, 14, 15, 16, and 18), or it focuses on individual species (e.g., Ch. 16) or phenomena (e.g., Ch. 4, Sect. 3, 8, 15, 17 and 18). Descriptions of ecosystem structure and dynamics, hydroperiod, and biogeochemistry are not abundant. Bruenig's work on the physiognomy of peat swamps (Ch. 13) and Myers' study of hydroperiod in Costa Rican palm swamps (Ch. 11) are exceptions. Collection of these kinds of data is critical for advancing the understanding of forested wetlands and for properly managing and assessing their role in the landscape. Experimental approaches on these ecosystems are fewer still. An example is the experiment with sewage enrichment of a basin forested wetland in Florida (Ewel and Odum, 1984).

This chapter reviews paradigms of "forested wetland ecology" and proposes patterns of ecosystem response which could be tested in the future. We refer the reader to Odum (1984) for an overview of what is known about cypress (*Taxodium*) wetlands, including detailed discussions of diurnal, seasonal, and long-term patterns of ecosystem function, regional role of wetlands, wetlands values, and human use. Odum's review covers many paradigms that apply to all types of wetlands and are not repeated here.

Our first proposal is that the principles of forested wetland ecology are the same as those for other wetland types (Brinson et al., 1981; Lugo, 1982). For this reason we use the term "wetlands"

in this chapter to mean all wetlands, and we modify the term with "forested" when referring to data sets or ideas unique to them.

THE ROLE OF HYDROLOGY

The available evidence strongly supports the idea that forested wetlands, like all other types of wetlands, develop more structure and are more productive under riverine conditions (Table 19.1). Low values of productivity and structural measures are associated with basin conditions, with the exception of tree density which is high in basin forests. Brown et al. (1979) suggested that this high stem density is a response to poor soil aeration. A higher stem density results in a higher surface area for gas exchange. Alternatively, higher tree density may be a result of lower tree mortality in basin wetlands where hydrologic fluxes are less potentially destructive. Fringe-wetland data are limited to mangrove forests, which are usually intermediate between riverine and basin mangrove forests in terms of structure and functional parameters (Cintrón et al., 1985).

Many investigators have identified relations between hydrological parameters and wetland response (e.g., Mitsch and Ewel, 1979; Connor et al., 1981; Gosselink et al., 1981). Ch. 16 by Specht develops a Moisture Index based on water-balance information to explain wetland physiognomy and regeneration. These relations support the general hypothesis of hydrologic control of wetlands. Even the substrate of wetlands is a function of the hydrologic regime (Ch. 4, Section 15, Fig. 4.10).

The direction and kinetic energy of water flow are critical factors in the regulation of wetland

TABLE 19.1 (continued)

Parameter (units)	Riverine		Fringe		Basin	
	fresh	salt	fresh	salt	fresh	salt
Potassium						
Range	17.0-30.6	—	—	—	3.3-9.5	—
<i>n</i>	4	—	—	—	5	—
Mean	22.3	—	—	—	5.4	—
Calcium						
Range	29.9-129.2	—	—	65-125	23-91	—
<i>n</i>	4	—	—	7	7	—
Mean	70.8	—	—	96.6	46.3	—
Magnesium						
Range	7.38-37.2	—	—	—	4.7-12.0	—
<i>n</i>	4	—	—	—	7	—
Mean	18.6	—	—	—	7.7	—

¹Data from Chapter 5 (Tables 5.1, 5.2, 5.3, 5.4, 5.6, 5.7), Chapter 6 (Tables 6.2, 6.3, 6.6, and 6.9) and Chapter 7 (Tables 7.3, 7.4, 7.7, and 7.11).

function. Direction of water flow (unidirectional, vertical, or bidirectional) separates riverine, basin, and fringe wetlands respectively, while the kinetic energy associated with the flow can either stress or subsidize the wetland (Ch. 3 and 6). Water motion is generally a subsidy for most wetlands because of the work it can do in the system (e.g., movement of nutrients, aeration, dispersal of propagules, ventilation of roots, etc.; Ch. 4, Sect. 17). There are few exceptions to this subsidy function, because species distribute themselves around hydrologic conditions to which they are adapted (cf. Fig. 11.8 in Ch. 11 by Myers for examples of how palms adjust to hydroperiod). However, if the hydrologic fluxes are too intense, they become stressful by exporting excessive amounts of materials (Frangi and Lugo, 1985), by causing physical damage to the ecosystem (Chs. 5, 17 and 18 give examples of floating ice damage to floodplain communities), and by reducing the time available to the system to take advantage of the materials in flux (Ch. 4, Sects. 6 and 21). In these cases, the lifetime of the wetland may be limited, the community will function suboptimally, or a less complex system will develop on the site.

While it is obvious that the hydrology of a typical basin wetland is different from that of typical riverine or fringe wetlands, local variations

in topography affect water flow, which in turn causes "mixtures" of wetland types. For example, within a large basin wetland (hundreds of hectares) one can identify "water tracks" (Heinselman, 1970), which behave like riverine wetlands. Similarly, protected sectors of riverine floodplains or the landward sectors of fringe wetlands, may behave like basin wetlands. In fact, a given area of wetland might behave as a basin system for part of the year and as a riverine system during another season.

These deviations from the "model" or idealized wetland types are not weaknesses in the concept of wetlands as presented here, but offer instead an excellent opportunity for enhancing understanding of these ecosystems. The three geomorphologic wetland types (fringe, riverine, and basin; Figs. 19.1-19.3) are fundamental functional units which can be identified in the field at scales ranging from individual trees responding to micro-edaphic factors to large regions such as the Great Dismal Swamp in the United States of America (Ch. 8). When the hydrologic regime is identified at the appropriate scale and a wetland type is assigned, the predictable behavior of that wetland allows researchers and managers to stratify research or management actions according to the mix of wetland conditions under consideration.

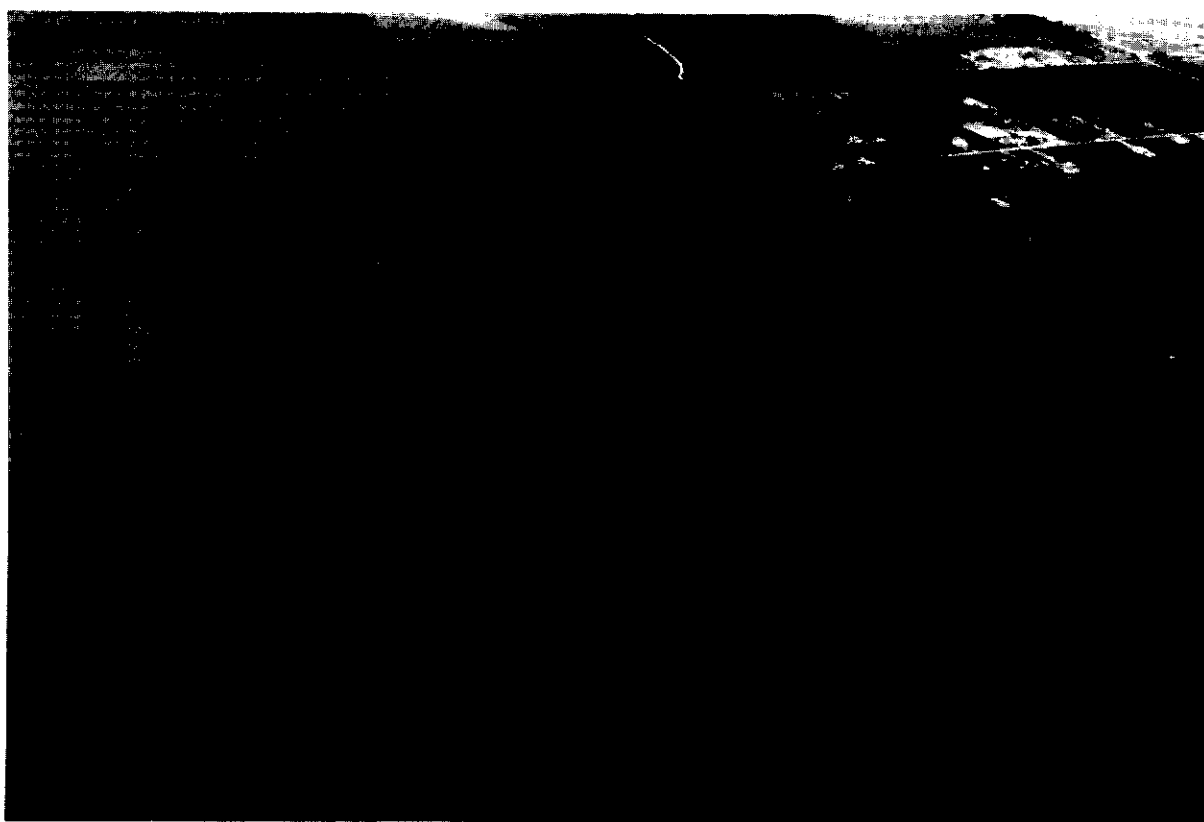


Fig. 19.2. Aerial view of a saltwater riverine forested wetland (mangroves). In this type of wetland tree zonation and ecosystem organization are parallel to the river's hydrologic energy (Chapter 5).

THE INFLUENCE OF NUTRIENTS

Hydrology by itself does not explain all the behavior of wetlands. Chapters 9, 12, and 13 use soil chemistry information to explain wetland physiognomy and complexity. Wetlands are part of a larger ecosystem or catchment whose configuration, geomorphology, and size affect the flux of materials (water, sediments, and nutrients) into the wetland. The quality and quantity of surface water and groundwater entering a wetland are a function of the size and landscape diversity of the catchment. The influence of water quality on wetlands has led many to classify wetlands into nutrient-rich and nutrient-poor types (eutrophic vs oligotrophic, or minerotrophic vs ombrotrophic). In fact, models that relate such wetland functions as primary productivity or tree growth to the interaction of hydrological and chemical characteristics of waters yield better correlations than single-factor models (Brown, 1981). Fig. 19.4 summarizes

Odum's (1984) interpretation of the synergism between hydrology and nutrient fluxes in Florida cypress wetlands. In this scheme, ecosystem complexity increases with increases in the flows of water and nutrients. Ch. 3 by Kangas elaborates on these concepts.

In spite of the scarcity of information, wetlands are characterized as nutrient-rich or nutrient-poor ecosystems by using water chemistry, peat depth, and physiognomy of vegetation (e.g., presence or absence of xeromorphy or sclerophylly). There is a need to consider the chemical aspects of wetlands in a more holistic context. The chemistry of wetland ecosystems is extremely complex as it involves aerobic as well as anaerobic processes. These processes in turn are closely coupled to atmospheric, hydrologic, and edaphic factors. Furthermore, plants respond to any or all of these chemical environments with a complex array of biotic adaptations that affect the speed and efficiency of nutrient uptake and use. For example,

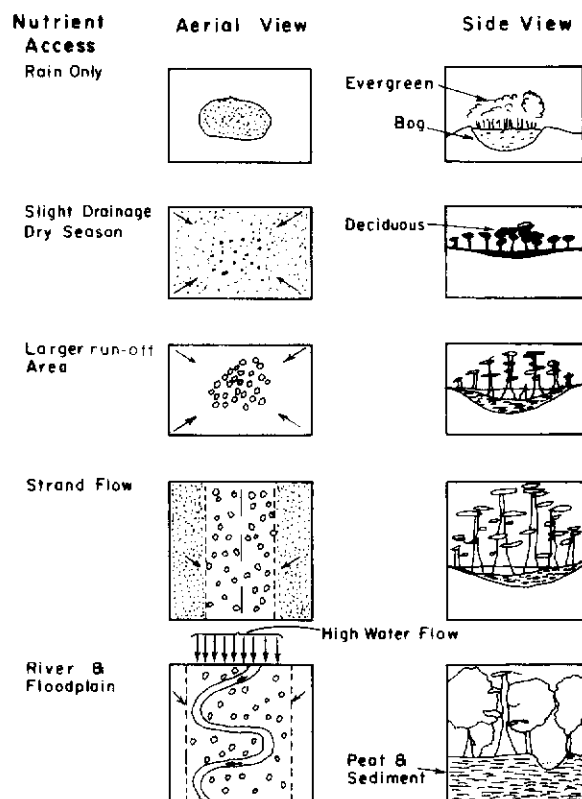


Fig. 19.4. Classification of cypress (*Taxodium*) wetlands of Florida, arranged in order of increasing water and nutrient flows from top to bottom (Ewel and Odum, 1984).

efficiency (Fig. 19.6) can be used to formulate the following generalizations:

(1) The recycling efficiency of calcium is low, suggesting that this element is not limiting to wetlands. However, Igapo riverine wetlands (black-waters) with acid, nutrient-poor waters, are the most efficient in the recycling of calcium. This suggests that in this type of environment calcium may be limiting. The same appears to be the case with black mangrove (*Avicennia germinans*) wetlands.

(2) The pattern of nitrogen recycling efficiency is better defined than that of calcium. Australian mangroves show a higher recycling efficiency than those from Malaysia, basin wetlands have higher recycling efficiency than riverine ones, and systems with *Laguncularia racemosa*, the white mangrove, have higher recycling efficiencies than any other species or wetland type shown. In addition, for a given rate of nutrient return by litter-fall, saltwater

wetlands appear to be more efficient than their freshwater counterparts.

(3) Most wetlands exhibit very high efficiencies of phosphorus recycling, suggesting that this element may be the main limiting factor of these ecosystems. However, freshwater wetlands are less efficient than saltwater ones for any given rate of phosphorus return by litter-fall. The pattern for phosphorus recycling efficiency shows less scatter than for calcium or nitrogen and also separates the efficient Australian mangroves from the less efficient ones in Malaysia. Scrub red mangroves (*Rhizophora mangle*) growing on marl in the Florida Everglades (Fig. 19.3), exhibit the highest phosphorus recycling efficiency of all systems studied.

We propose that the efficiency of nutrient cycling in ecosystems can be calculated with a variety of indices derived from Fig. 19.5 (Table 19.2), and that depending upon conditions any or a combination of these indices may be reflecting the "true" efficiency of the ecosystem. For example, Frangi and Lugo (1985) found that an eroding floodplain forest in Puerto Rico was exporting more phosphorus than it received from upstream sources, and was losing large amounts of phosphorus due to leaching from the canopy and soils (i.e., it was inefficient in terms of inputs-outputs and Pathway 3). However, its within-stand efficiency of phosphorus recycling (Pathway 4) and rate of phosphorus retranslocation (Pathway 2) were extremely high. This example illustrates two points: (1) the importance of identifying boundaries and limitations to nutrient-cycling studies; and (2) that high efficiency of biotic recycling may be a response to environments where abiotically-controlled recycling efficiencies are low. A corollary hypothesis is that the biotically-controlled recycling efficiency is low in environments where the abiotically-controlled recycling efficiency is high.

Hydrologic and nutritional factors must be considered when explaining the degree of nutrient recycling in a given type of wetland. As an example, the turnover of litter will be considered. Hydrologic forces will be instrumental in determining the residence time of litter on the forest floor, while nutritional factors affect the rate of microbial degradation. It appears that wetlands with fast water turnover are characterized by high rates of nutrient turnover and low litter accumulation.

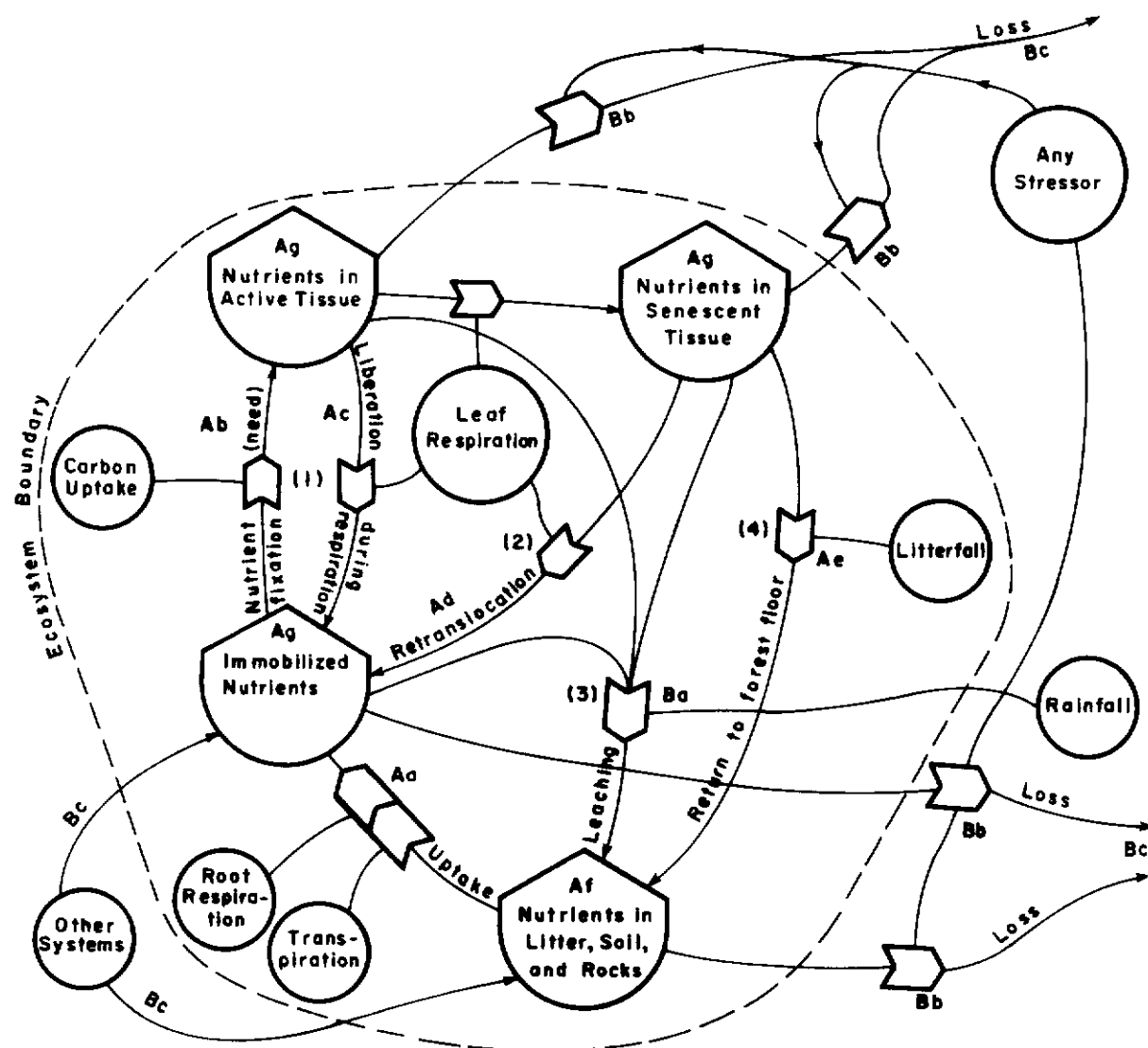


Fig. 19.5. Model of nutrient cycling in forested ecosystems. The ecosystem boundary is the broken line. Tanks represent state variables, circles represent the biotic and abiotic factors believed responsible for the nutrient flux, and the arrow-shaped symbols show interactions of a nutrient flux and its control factor (Ch. 4, Sect. 9 explains the symbols). The ratio of control factor to nutrient flux is an index of recycling efficiency. Number codes relate to pathways mentioned in the text; letter codes are keyed to Table 19.2.

the value of landform is amplified considerably. This latter value is more realistic, as it takes much more energy to replace landform than it does to replace ecosystem biomass. Table 19.3 is another example from Odum (1984) illustrating the embodied energy passing through and being used by the cypress swamp ecosystems illustrated in Fig. 19.4. As energy availability increases, its efficiency of use is lower but more work is done, measured in this case in terms of transpiration (Table 19.3)

or the maintenance of ecosystem complexity (Fig. 19.4).

In spite of the absence of an extensive data base, wetlands can be categorized by a multi-factor approach using the most important variables in the energy signature. We believe that such variables are kinetic energy of water in motion, the chemistry of the ecosystem measured in terms of nutrient availability (exogenous sources) and turnover (internal dynamics), and the hydroperiod (season,

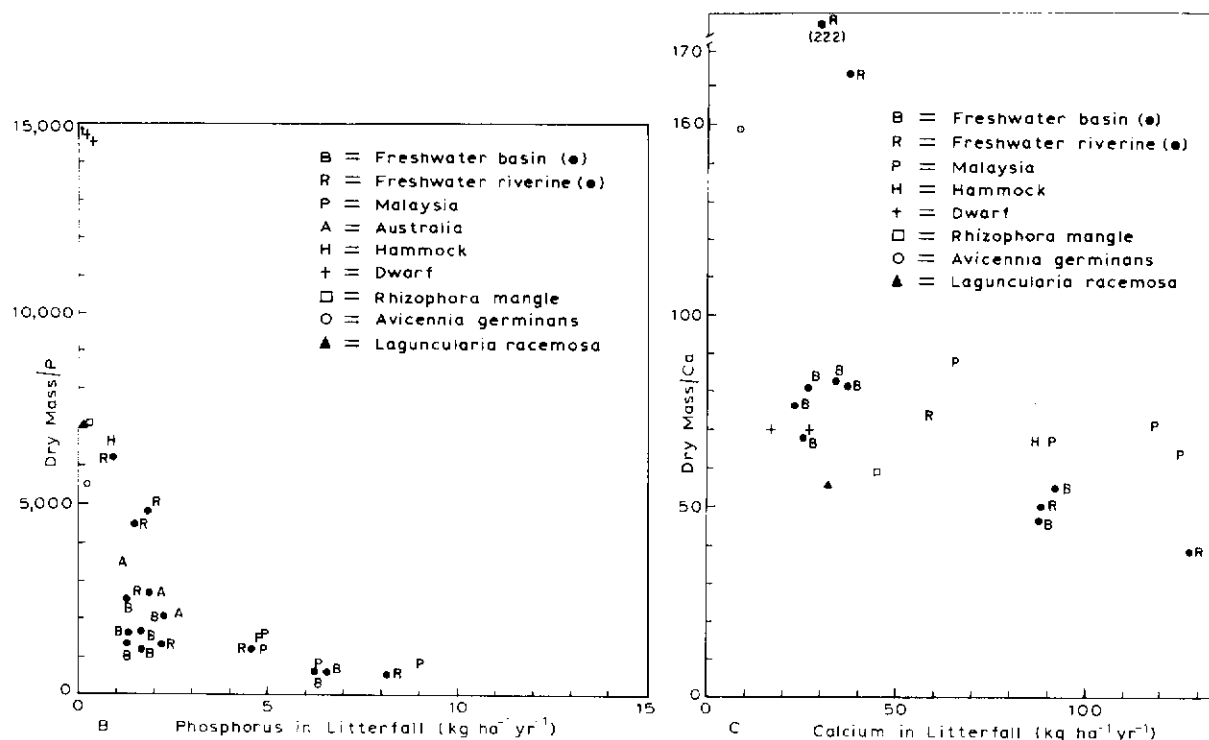


Fig. 19.6. The relation between within-stand recycling efficiency ratio and nutrient return in litter-fall for freshwater and saltwater forested wetlands. Data are mainly for mangrove wetlands, unless stated. Sources are Chapters 5, 7 and 18 for freshwater wetlands and from many sources for mangroves (available from A.E. Lugo).

TABLE 19.3

Embodied energy of swamps with increasing water availability. Wetland types are in the same order as those in Figure 19.4 (This table is from Ewel and Odum, 1984.)

Item	Water processed ¹ (m ³ m ⁻² yr ⁻¹)	Transpiration ² (m ³ m ⁻² yr ⁻¹)	Embodied energy passing through ³ (GJ m ⁻² yr ⁻¹)	Embodied energy used, global solar ⁴ (GJ m ⁻² yr ⁻¹)
Direct sunlight	—	—	42	36
Rain only, bays	2	0.3 ⁵	678	100
Dwarf cypress	4	0.34 ⁶	1364	117
Pond cypress	8	1.12 ⁶	2720	381
Strand cypress	40	1.5 ⁵	13 640	510
Floodplain	100	1.89 ⁶	34 058	640

¹The amount of water passing through the wetlands.

²1 m³ m⁻² yr⁻¹ = 2.74 mm day⁻¹

³Embodied energy is defined in Chapter 3, and is expressed as GJ m⁻² yr⁻¹ (1 GJ = 239 Mcal) The figures in this column are embodied energy per unit volume multiplied by the water passing. Embodied energy per unit volume = $(1.18 \times 10^{-3} \text{ cal g actual free energy in rain}^{-1}) (6.9 \times 10^4 \text{ global solar equivalent cal cal}^{-1}) = 8.1 \text{ global solar cal g water}^{-1}$.

⁴These figures are embodied energy per unit volume multiplied by the water used in transpiration.

⁵Calculated by interpolation.

⁶Brown (1981).

Because some wetlands also export significant amounts of organic carbon in run-off (Ch. 4, Sect. 2), they can simultaneously serve as carbon sinks for the atmosphere and carbon sources for downstream ecosystems.

For nitrogen, there can be significant exchanges across both boundaries, and the magnitude may depend on the geomorphic setting. Riverine wetlands exchange water-borne inorganic nitrogen with the landscape, in addition to having significant atmospheric exchanges (Brinson et al., 1983). Basin wetlands are restricted to predominantly wetland-atmospheric exchanges through nitrogen fixation and denitrification pathways, while fringes are probably intermediate between the other two types of wetlands. Because of the difficulty of measuring with confidence the in-situ rates of nitrogen fixation and denitrification, one is far from achieving a holistic perspective on the nitrogen cycle in wetlands. For example, one knows that wetlands have the potential to absorb large amounts of nitrate and to lose this nitrogen source through denitrification. Yet, this potential is seldom realized because of limits in the rate of nitrate supply (Ch. 4, Sect. 18). A more holistic perspective is that basin wetlands accumulate nitrogen through peat-building processes, and that riverine wetlands are dynamic transformers between organic and inorganic forms (Elder, 1985). As with carbon, a wetland can simultaneously serve as a sink for atmospheric and upstream nitrogen (through peat accumulation), and a source of organic nitrogen compounds for downstream ecosystems.

The behavior of phosphorus is simpler at the ecosystem level because it has no atmospheric sink. Atmospheric sources of phosphorus are significant only in strictly ombrotrophic basins. Riverine wetlands rely predominantly on landscape sources, while fringe ones depend on the water body that they fringe, together with any landscape or groundwater sources to which they may be coupled. All types accumulate phosphorus unless they switch to a nonsedimentary regime. In such cases, the lifetime of an eroding wetland is limited.

The significance of sulfur lies not in a potential for nutrient limitation, but in its influence on organic-matter decomposition, its capacity to modify the sediment environment, and its function in detritus food webs. Because sulfur is so much

more abundant in saltwater than freshwater wetlands, generalizations about its behavior (Ch. 4, Sect. 18) are best limited at this time to distinguishing between these two types rather than seeking patterns among riverine, fringe, and basin types.

Appreciation of the differing behavior of elements among themselves and among wetland types allows some speculation on the potential for nutrient limitation in primary productivity. Because the source of carbon is strictly atmospheric, and the atmospheric pool is unlimited, arguments for carbon limitation are trivial. For nitrogen and phosphorus, some insight into nutrient limitation is possible at the ecosystem level. Basin wetlands receive both nitrogen and phosphorus mainly from atmospheric sources, by fixation and precipitation in the case of nitrogen and from precipitation only for phosphorus. Strategies for adapting to limitations by these two elements differ. For phosphorus the only strategy is through mechanisms of recycling, because the ecosystem has no control over the abiotic source. This strategy is evident in Fig. 19.6 where the within-stand recycling efficiency of phosphorus is shown to be high in many wetlands.

For nitrogen, the atmospheric source is unlimited (N_2) and the strategy available is nitrogen fixation. Because nitrogen fixation has both an energetic cost and a stimulatory effect on wetland production, there are limits to the amount of nitrogen that can be fixed. Assuming that the ecosystem can compensate for nitrogen deficiency through nitrogen fixation, it is more likely that basins will be limited by phosphorus than by nitrogen. This is supported by the relative within-stand recycling efficiencies of phosphorus and nitrogen in Fig. 19.6, and by the low efficiency of nitrogen recycling by alder wetlands in Poland (the lowest ratio reported, i.e., 43: Ch. 18). Many riverine wetlands have abundant sources of phosphorus through accumulation of inorganic sediments from the landscape (Table 5.8). Like basin wetlands, they also have access to unlimited supplies of atmospheric nitrogen. We postulate that nitrogen and phosphorus limitation in many riverine forested wetlands is not a critical factor. Energy in riverine forests can be allocated toward other adaptive functions. The biomass of many riverine forests (Table 19.1) suggests that plenty of energy is being allocated to the building of